A NEW CONIFER GENUS FROM THE LOWER CRETACEOUS GLEN ROSE FORMATION, TEXAS

by JOAN WATSON *and* HELEN L. FISHER

ABSTRACT. A new genus, *Glenrosa*, is erected to include two species of fossil conifer shoots, *G. texensis* (Fontaine) comb. nov. (the type species) and *G. pagiophylloides* (Fontaine) comb. nov. which are found interspersed with conifer species belonging to the family Cheirolepidiaceae. The stomatal arrangement of the new genus, which is similar to that of the extant angiosperm *Nerium oleander* L. of the Apocynaceae but unlike any other gymnosperm, shows extreme xeromorphy and is probably an adaptation to an arid environment.

THE flora of the Lower Cretaceous Glen Rose Formation in central Texas, which was first described by Fontaine (1893), comprises some five or six well-characterized conifers together with two or three bennettitalean species and a number of cones which have not yet been satisfactorily attributed to parent plants. The original collection on which Fontaine worked was made by Mr. J. W. Harvey of Glen Rose and is now housed in the Smithsonian Institution. The specimens are few in number and mostly fragmentary but the cuticles are exquisitely preserved in the fine dolomitic limestone. This small but important flora is currently being revised and continues to yield surprising results. Two of the conifers which have already been redescribed (Watson 1977) proved to be members of the extinct family Cheirolepidiaceae. Both species, *Frenelopsis alata* (K. Feistmantel) Knobloch and *Pseudofrenelopsis varians* (Fontaine) Watson have a most unusual jointed, xeromorphic appearance and *P. varians* has an extraordinary cuticle well over 100 μm thick. The two conifers redescribed below, whilst not unusual in morphology, have proved to possess a stomatal arrangement unique amongst conifers.

SYSTEMATIC PALAEONTOLOGY

The microscope preparations are housed with their parent specimens in the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Hunterian Museum, Glasgow. A duplicate set of preparations has been deposited in the British Museum (Natural History) (numbers V58652–V58653).

CONIFERALES *incertae sedis*
Genus *Glenrosa* gen. nov.

Type species. Brachyphyllum texense Fontaine, 1893, p. 269.

Diagnosis. Coniferous tree or shrub with spirally arranged leaves, adpressed or falcate. Stomata occurring in groups, each group confined to sunken chamber which forms communal stomatal pit narrowing towards rim.

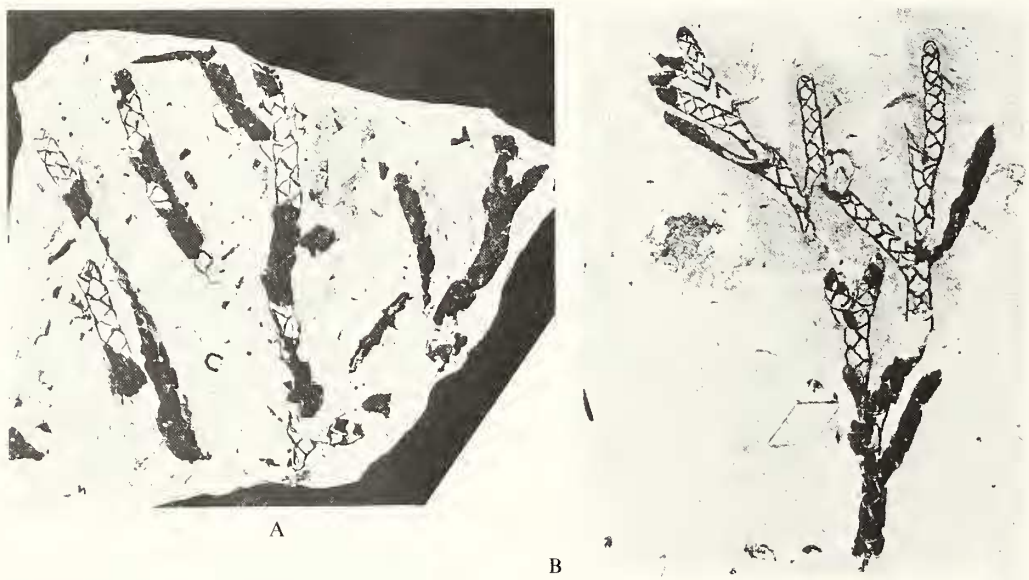
Glenrosa texensis (Fontaine) comb. nov.

Plate 64; text-figs. 1, 2, 4A

1893 *Brachyphyllum texense* Fontaine, p. 269, pl. 38, fig. 5; pl. 39, figs. 1, 1*a*.

[Palaeontology, Vol. 27, Part 4, 1984, pp. 719–727, pls. 64–65.]

Emended diagnosis. Branched shoots bearing leaves in a simple helix with 1 + 2 parastichies. Leaves scale-like, adpressed, arising from centre of rhomboidal leaf-base cushion; leaf and basal cushion combined typically 3 mm long and 2·5 mm wide. Free part of leaf up to one fifth of total length. Leaf margins converging at up to 70° towards bluntly pointed apex; fimbriate, hairs up to 65 μm long. Leaf biconvex in section with prominent median keel on abaxial surface continuing onto cushion. Stomatal chambers oval, occurring on both surfaces; four to eight stomata per chamber; long finger-like processes interdigitating across opening of chamber. Abaxial chambers scattered over whole surface, up to eight per square mm; typically 112 μm long and 69 μm wide. Adaxial chambers smaller, arranged in well-spaced curving row, inset from but following leaf margin; typically 90 μm long and 66 μm wide. Stomatal apparatus commonly 75 μm long and 50 μm wide with four to six subsidiary cells, sometimes shared between adjacent stomata. Ordinary epidermal cells of both surfaces rectangular, arranged in longitudinal files converging at apex; average size 38 μm long and 16 μm wide. Anticlinal walls straight, pitted, up to 5 μm wide. Well-developed cutinized hypodermis of elongated cells present under non-stomatal areas.



TEXT-FIG. 1. *Glenrosa texensis* (Fontaine). A, USNM 326800, lectotype, × 1. B, USNM 326801, the other branched specimen previously figured by Fontaine, × 1. The leaf outlines on both of these specimens are now known to be indian ink.

EXPLANATION OF PLATE 64

Figs. 1–7. *Glenrosa texensis* (Fontaine). 1, 4–6 are scanning electron micrographs. 1, USNM 192358, single leaf showing scattered stomatal chambers on inside of abaxial surface and the outside of part of the adaxial surface, × 25. 2, USNM 192384, light micrograph of similar leaf, × 25. 3, Pb 2093, part of adaxial cuticle showing curving row of stomatal chambers, × 100. 4, USNM 192358, part of fig. 1 showing the fimbriate margin and the stomatal chambers, × 100. 5, USNM 326800, outside of abaxial surface showing interdigitating papillae sealing stomatal chamber, × 200. 6, USNM 192358, outer view of single adaxial stomatal chamber showing details of finger-like papillae, × 400. 7, Pb 2093, light micrograph of single abaxial stomatal chamber showing papillae arising around rim; stomata missing, × 400.

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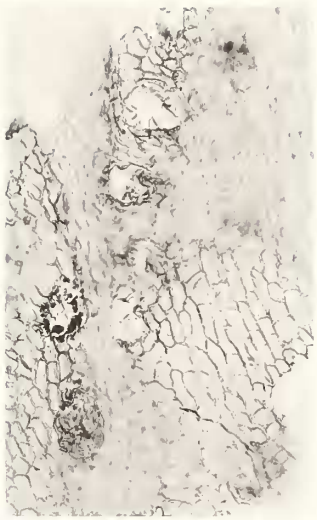

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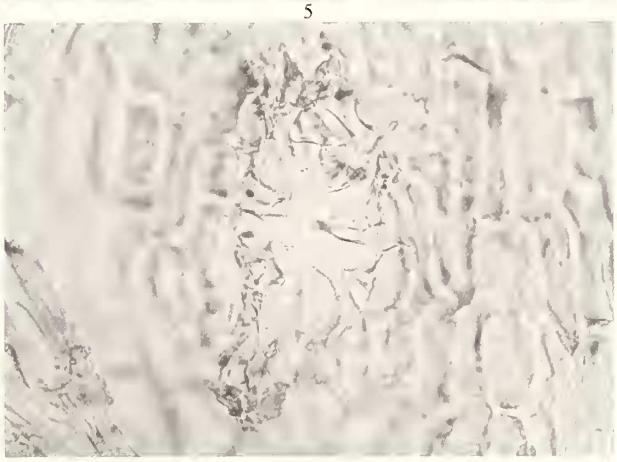

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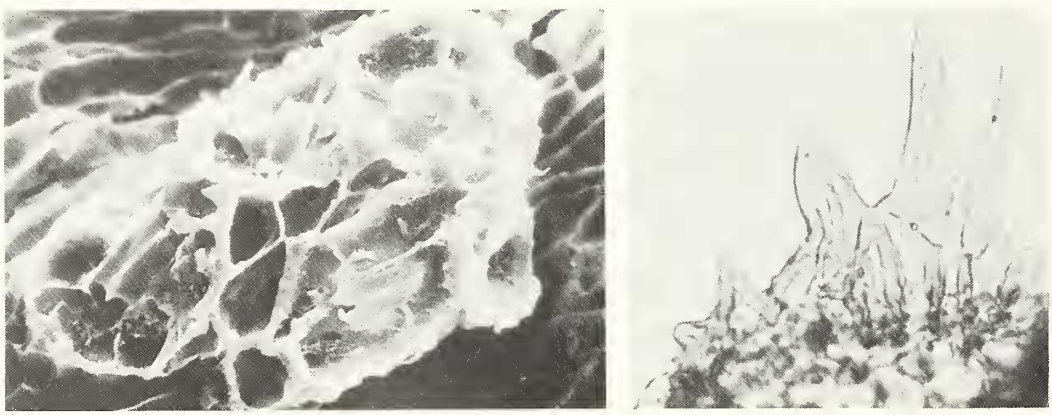
WATSON and FISHER, *Glenrosa*

Material and occurrence. The lectotype USNM 326800 was figured by Fontaine (1893, pl. 38, fig. 5). *G. texensis* (Fontaine) is known from two localities in the U.S.A.: Glen Rose, Texas, the type locality which yielded excellent specimens, and Trent's Reach, Virginia, from where very short lengths of shoot have been identified. The Glen Rose Limestone in the Trinity Group (Lower Cretaceous) is considered to be late Aptian to earliest Albian. The Trent's Reach locality has been dated as Barremian to Aptian. The total Smithsonian collection of this species numbers only five specimens, plus a number of cones which could prove to belong to it. All the cones are from Glen Rose. Specimen Pb 2093 from Trent's Reach is in a small collection of fossil plants bearing old Smithsonian numbers in the Hunterian Museum, Glasgow (see Watson 1977, p. 718).

Description. It should be pointed out that the leaves showing only as black outlines, previously figured by Fontaine (1893) and refigured here as text-fig. 1, were at first assumed to have rims of cuticle remaining, and the diagnosis was made on this assumption. It is now clear, however, that they are drawn in, probably in indian ink and presumably by Fontaine. There is no reason to suppose that they are not accurately drawn, as the impressions left by the bulging leaves and bases are very clear. The persistent leaves have cuticle which is thick, beautifully preserved and macerates easily and quickly; as a result several preparations of whole leaves could be obtained without difficulty. Plate 64, fig. 1 clearly shows the stomatal chambers of *G. texensis* scattered over the whole of the abaxial surface and ordered in a well-spaced curving row following the leaf margins on the adaxial surface. The outside surface of the cuticle viewed with the SEM (Pl. 64, figs. 4–6) shows papillae around the rim of the stomatal chamber interdigitating and effectively sealing the opening. It is clear from Plate 64, fig. 7 that some of these finger-like protuberances are borne by certain epidermal cells around the rim of the chamber. In this preparation the inner parts of the chamber, including all the stomata, are missing. In preparations with complete chambers it was much more difficult to establish that at least some of the subsidiary cells also bear these

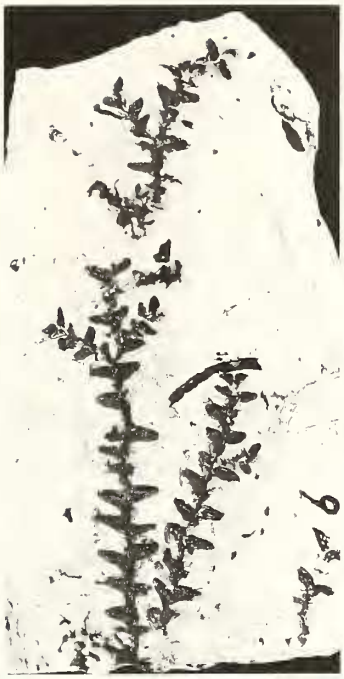


A B

TEXT-FIG. 2. *Glenrosa texensis* (Fontaine). A, USNM 326800, inside of abaxial cuticle showing details of a single group showing four stomata, ×400. B, USNM 192358, the longest hairs seen on the leaf margin, ×400.

EXPLANATION OF PLATE 65

Figs. 1–5. *Glenrosa pagiophylloides* (Fontaine). 3, 4 are scanning electron micrographs. 1, USNM 326803, one of Fontaine's figured specimens showing particularly large and well-shaped leaves, ×1. 2, USNM 326802A, lectotype showing branching pattern, ×1. 3, USNM 326802A, distal portion of leaf showing strongly papillate surface; openings of stomatal chambers are just visible scattered over surface, ×50. 4, USNM 192377, light micrograph showing long pointed hairs on ordinary epidermal cells, ×400. 5, USNM 192377, light micrograph showing distribution of stomatal chambers, some with stomata present, some without; cutinized hypodermis can be seen top left, ×100.



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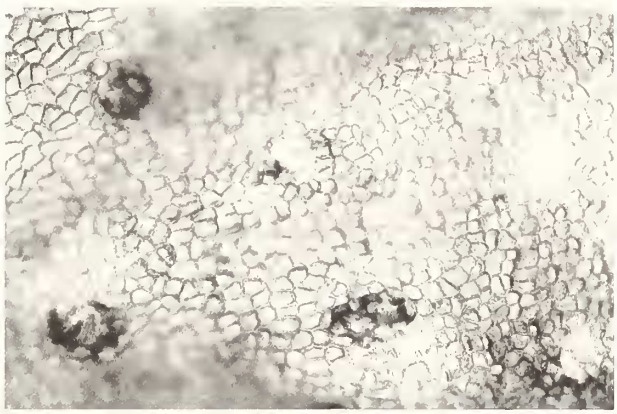

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papillae. This was done by viewing cut edges of cuticle at very high angles of tilt in the SEM. Text-fig. 4A is a reconstruction of a stomatal chamber in vertical section compiled from several of these SEM views.

The specimens from the two known localities show minor differences in that the Glen Rose specimens have slightly darker cuticle and a higher stomatal density. The shoots of *G. texensis* on the Trent's Reach blocks, particularly USNM 192358, are present as very short lengths amongst larger shoots of the conifer *Pseudofrenelopsis parceramosa* (Fontaine) Watson. Fontaine (1889, p. 220) stated in his description of *P. parceramosa* that it is found in close association with *Brachyphyllum crassicaule* Fontaine with few other species present. Clearly Fontaine considered all the small fragments to be *B. crassicaule*, not surprisingly since *G. texensis* was detected initially only in cuticle preparations. The Trent's Reach *G. texensis* has been used to illustrate cuticle features on Plate 64. The cuticle of *B. crassicaule* is clearly distinct and will be described elsewhere.

Glenrosa pagiophylloides (Fontaine) comb. nov.

Plate 65; text-figs. 3, 4B

1893 *Sequoia pagiophylloides* Fontaine, p. 276, pl. 42, figs. 1–3*a*.

Emended diagnosis. Branched twigs bearing falcate leaves diverging radially, standing away from axis at 80° or less. Free leaf up to 3 mm long, 2 mm wide at base tapering to acute, rounded apex, triangular in cross section; lower angle forming median keel continuing onto cushion, upper surface flat, leaf margins sharp, entire. Cuticle of all surfaces up to 10 μm thick. Stomatal chambers scattered over all surfaces, up to four stomata per chamber. Subsidiary cells of adjacent stomata often shared, some bearing long pointed papillae. Stomatal chambers having more or less circular rim, averaging 78 μm diameter, up to seven per square mm. Ordinary epidermal cells of both surfaces small, polygonal, randomly arranged; each bearing a small papilla. Average cell size 28 μm long and 23 μm wide. Anticlinal walls straight, pitted, up to 5 μm wide.

Material and occurrence. The lectotype USNM 326802A was figured by Fontaine (1893, pl. 42, fig. 1). *G. pagiophylloides* (Fontaine) is known only from the Glen Rose Limestone in the Trinity Division of the Lower Cretaceous at Glen Rose, Texas. The stratigraphic horizon is probably late Aptian to earliest Albian. The Smithsonian collection comprises some ten specimens of *G. pagiophylloides* including both part and counterpart of the lectotype.

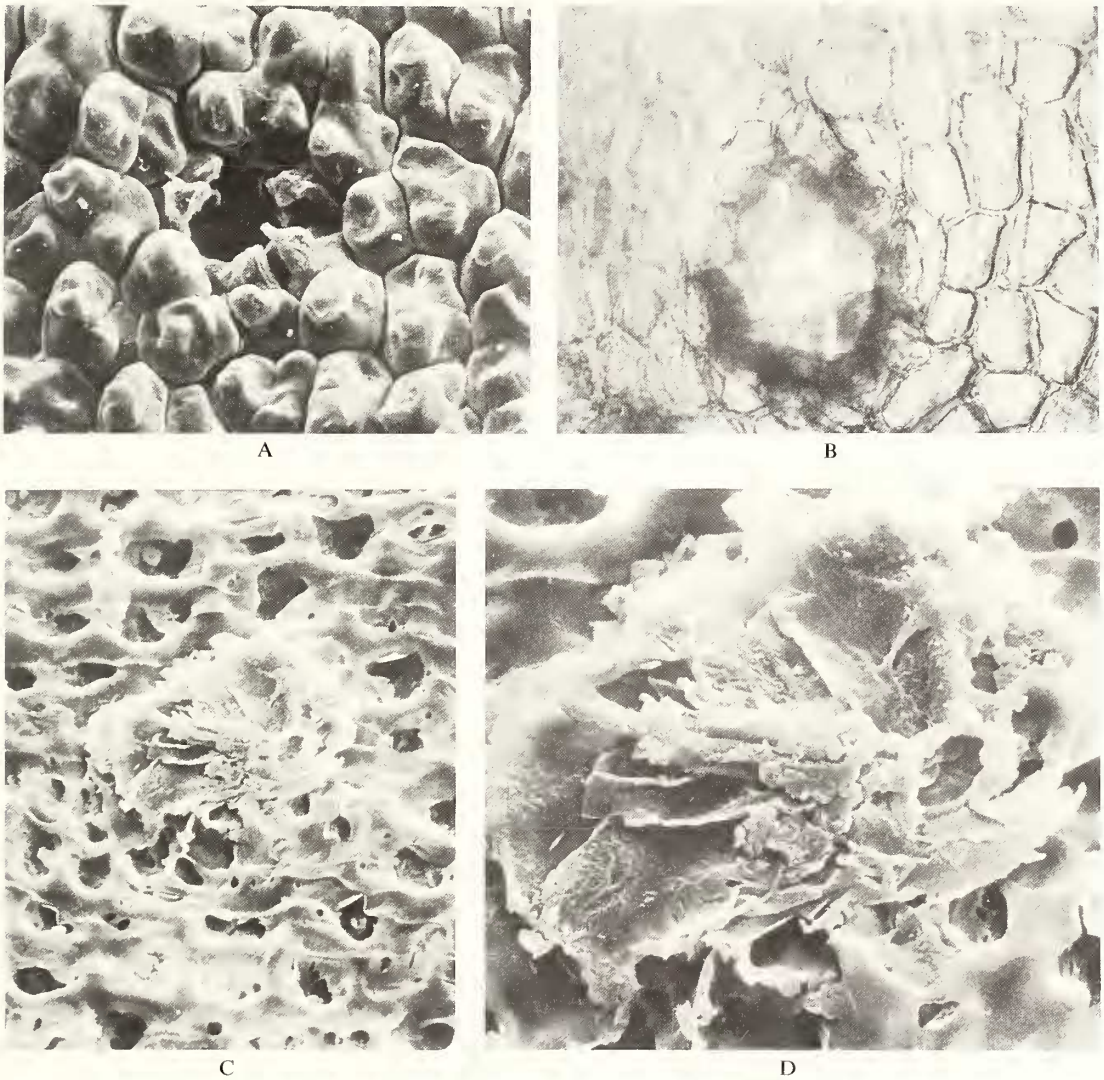
Description. The lectotype of *G. pagiophylloides* shows three orders of branching which appear alternate in one plane but we cannot say whether the shoots are truly complanate; nor are we able to determine the phyllotaxy. Fontaine (1893, pl. 42, fig. 1*a*) speaks of and illustrates inconspicuous facial leaves and much larger lateral leaves but we have been unable to confirm this. The axial parts of the shoots are rather crumbly and the facial leaves appear to us only as split and worn remnants. One would need to reveal the other side of a shoot by the transfer technique to be absolutely certain on this matter. Fontaine (1893, pl. 42, fig. 2*a*) also illustrates a double lateral keel on the leaves seen in side view, shown here in Plate 65, fig. 3. This is, however, an inconsistent feature which may well be a preservational effect.

The cuticle of *G. pagiophylloides* is very tough and easy to prepare though requiring a lengthy maceration time (up to twenty four hours). The surface of the leaf is extremely uniform, each cell bearing a short blunt papilla, but in one preparation some of the ordinary epidermal cells (Pl. 65, fig. 4) bear rather longer pointed hairs like those borne around the stomatal chamber. As with *G. texensis*, the exact configuration of the various cells and papillae within the stomatal chamber was very difficult to determine. The same technique of viewing cut edges in the SEM was used to draw up the reconstruction of a chamber in vertical section (text-fig. 4B).

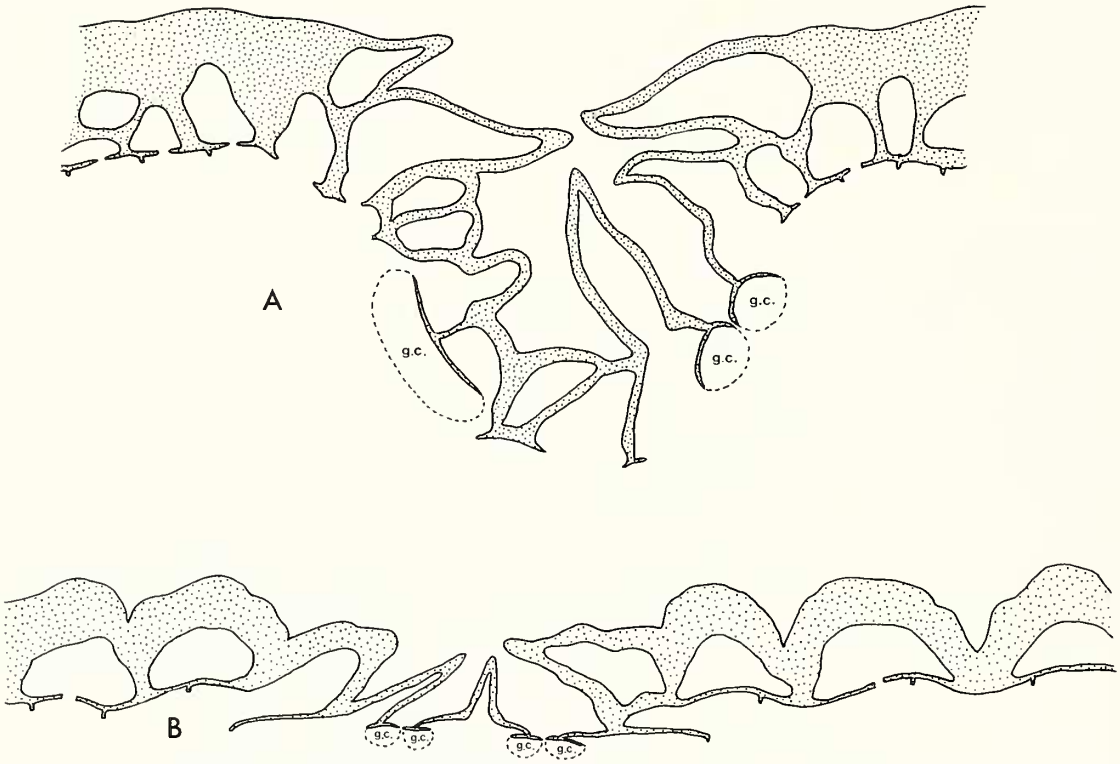
DISCUSSION AND COMPARISON

This interesting and unusual stomatal arrangement shown by *G. texensis* and *G. pagiophylloides* is unknown in any other conifer, fossil or living, and hence they can only be compared with each other. Confronted by two species of such a genus in the same flora, the possibility has not eluded us that they may represent adult and juvenile foliage of the same plant. All available specimens, however, are clearly distinct both in hand specimen and microscopically, and any such connection remains to be demonstrated.

The only other conifer we regard as even faintly reminiscent of *Glenrosa* is *Sphenolepis kurriana* (Dunker) Schenk from the Wealden of Germany and England which was recently revised by Fisher (1981). The stomatal chambers of *Glenrosa* could perhaps represent an extreme modification of the dense stomatal patches shown by *S. kurriana*. The *Glenrosa* form of stomatal distribution is most similar to that of the angiosperm *Nerium oleander* L. (Apocynaceae) but that species has much bigger stomatal chambers incorporating a larger number of specialized papillate epidermal cells than in the



TEXT-FIG. 3. *Glenrosa pagiophylloides* (Fontaine). A, C, D are scanning electron micrographs. A, USNM 326802A, outer surface showing papillae on ordinary epidermal cells and long hair-like papillae of subsidiary cells around opening of stomatal chamber, ×400. B, USNM 192377, light micrograph showing subsidiary cell papillae in and around stomatal chamber, ×400. C, USNM 326802, inner surface of cuticle showing cutinization of epidermal and hypodermal cells together with one stomatal complex, ×400. D, detail of fig. C clearly showing two sets of guard cells, at least one other stoma obliterated, ×1000.



TEXT-FIG. 4. A, *Glenrosa texensis* (Fontaine), reconstruction of vertical section of cuticle, ×700. B, *Glenrosa pagiophylloides* (Fontaine), reconstruction of vertical section of cuticle, ×700. Guard cells indicated by g.c.

conifer species. Thus the stomata of *N. oleander* are uncrowded and rarely share subsidiary cells. *N. oleander* is a classic textbook example of a species which has adapted to a hot, dry habitat. The stomatal spaces trap and contain still, humid air and in this way restrict the evaporation of trapped moisture. *G. texensis* shows further morphological adaptation to aridity by reduction to a scale-leaf whereas *G. pagiophylloides* has spreading leaves which potentially present a greater evaporation surface. This is compensated for by the papillae on the epidermal cells which would have contained the spread of trapped droplets of moisture on the surface, thus reducing the surface area available for evaporation.

The stomatal adaptation of *N. oleander* gives an indication of the type of habitat which *G. texensis* and *G. pagiophylloides* might have occupied. The *Glenrosa* species are found in association with the conifers *Frenelopsis alata*, *Pseudofrenelopsis parceramosa* and *P. varians* of the Cheirolepidiaceae; all five species showing extreme adaptation to arid conditions (Watson 1977). There is clear geological evidence (Daghlian and Person 1977) that the Glen Rose Formation represents an environment characterized by high salinity and high rates of evaporation.

The taxonomic position of *Glenrosa* can only be speculated upon at this stage but the family Cheirolepidiaceae must be a prime candidate. Research in recent years (Upchurch and Doyle 1981; Watson 1982) has shown that members of this family, characterized by the possession of *Classopollis* pollen, probably embraced a wide variety of habit and habitat with most species displaying extreme xeromorphic cuticle characters. It is possible that work about to commence on the dispersed cones in the Glen Rose flora will shed light on the affinities of *Glenrosa*.

Acknowledgements. We are most grateful to Mr. James P. Ferrigno of the Smithsonian Institution for photographs of the hand specimens and to Mr. Ian Miller of Manchester University for printing all the micrographs. H.L.F. acknowledges tenure of a N.E.R.C. studentship and J.W. thanks the Royal Society of London for a grant towards the cost of a visit to the Smithsonian Institution, Washington, D.C. A donation from the W. H. Lang Fund, Manchester University has helped towards the cost of the plates in this paper.

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Typescript received 22 July 1983
Revised typescript received 13 February 1984